

INTRASEXUAL AGGRESSION IN *METRIDIUM SENILE*

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ABSTRACT

The dioecious anemone *Metridium senile* reproduces both sexually (in summer) and asexually (year round). Asexual reproduction yields genetically identical clones via longitudinal fission or pedal laceration. Clonemates may form large aggregates, ranked together in close order, and become aggressive against neighboring clones. Interclonal aggression is frequently carried out with the use of hypertrophied tentacles referred to as catch tentacles. The present study indicates that catch tentacles do not maintain clonal segregation, and do not serve as aggressive appendages against all nonclonemates. Laboratory pairings of nonclonemates and observations of their movements in the field indicate that interclonal aggression in this species is mediated by sex. Nonclonemates will become aggressive only against same sexed individuals, males fighting males and females fighting females, while nonclonemates of opposite sex may exhibit nonaggressive interaction, with or without the use of catch tentacles. Interclonal/intrasexual aggression in this species may function to increase the probability of successful fertilization during sexual reproduction by increasing the proximity of males to females and *vice versa*.

INTRODUCTION

Metridium senile is a dioecious cold water anemone common on both the east and west coasts of the United States. *Metridium* reproduces both sexually (in summer) and asexually (year round) by pedal laceration and longitudinal fission (Stephenson, 1935). Asexual reproduction commonly produces clones ranging from a few to many hundreds of genetically identical individuals. Color variation among clones makes it possible to distinguish easily between clonemates and nonclonemates in the field (Hoffman, 1976).

Most populations include individuals bearing large opaque tentacles surrounding the mouth which are structurally and functionally distinct from feeding tentacles (Purcell, 1977). Prior studies have shown that these tentacles, referred to as "catch tentacles" may be used in aggressive encounters between nonclonemates. These appendages, derived from feeding tentacles though not themselves used in feeding, had originally been reported to function in the maintenance of interclonal boundaries, in much the same way as acrorhagi maintain interclonal segregation in *Anthopleura elegantissima* (Francis, 1973). Intermingling of clones among *Metridium* is not uncommon, and individuals of clearly distinct appearance, bearing catch tentacles, are frequently found adjacent and in contact in the field (Purcell and Kiting, 1982), with no sign of aggressive interaction.

Interclonal aggression may be initiated when an individual spontaneously extends catch tentacles and contacts a nonclonemate, or when movement within or between clones bring two nonclonemates within feeding tentacle range. When extended, catch tentacles are longer than feeding tentacles, and may be as much as four times longer than the diameter of the oral disc (Purcell and Kiting, 1982),

extending the effective territory of the anemone by a factor of eight. When a catch tentacle finds a nonclonemate and nematocyst discharge occurs, the tentacle tip may adhere, while the tentacle retracts, so that the tip breaks off and remains attached to the victim, continuing to sting after the aggressor has withdrawn. Following one or more bouts of aggressive interaction, one anemone will usually retract its tentacles within its column, and bend or move across the substrate, out of range of further attack. Interclonal contact without aggressive interaction may also involve catch tentacle extension. Nonclonemates may contact one another with catch tentacles, draw closer, make contact with feeding tentacles, and remain in close proximity with no aggression or withdrawal, sometimes for days.

The present study tests the hypothesis that catch tentacles are used in aggressive interaction exclusively between nonclonemates of like sex, and that nonclonemates of opposite sex not only tolerate one another's presence but may engage in non-aggressive interaction.

MATERIALS AND METHODS

Seventeen anemones from five clones with catch tentacles (two male and three female clones) were collected from Monterey Harbor and the Elkhorn Slough, and allowed to settle on individually marked glass discs in flowing sea water aquaria. Each subject was anesthetised in an isotonic magnesium chloride solution to facilitate examination of the contents of the gastrovascular cavity. A glass pipette was introduced into the oral opening, and its contents withdrawn. In some cases the wall of the gastrovascular cavity was pierced and cellular material withdrawn from within. All subjects contained either live sperm or well developed eggs. In this manner it was possible to determine the sex of the individual without resorting to the more conventional sectioning and staining techniques which make subsequent behavioral testing difficult.

Two individuals from different clones were placed in contact with one another in sea water-filled glass observation bowls. Trials lasted up to twelve hours. Aggressive contact was clearly distinguishable from nonaggressive interaction as it was quickly followed by marked, sharp withdrawal as if in response to pain. In some cases aggressive interaction began immediately upon contact. In others it appeared only after hours of intermittent contact and withdrawal. Aggressive behavior, *i.e.*, first catch tentacle erection, number of catch tentacles erect, and elapsed time until separation, were recorded. Eighteen of forty-two pairings elicited catch tentacle expansion. Eleven of these were aggressive encounters.

Following forty-two laboratory pairings all subjects were allowed to settle on a Plexiglas panel which was then suspended in Monterey Harbor, so that the anemones could move freely, contacting clonemates and nonclonemates of both sexes on the basis of "preference." The position and movement of each anemone was checked and recorded daily for an eighteen day period.

RESULTS

Forty-two trials were conducted, in which twelve individuals showed aggressive behavior. All instances of aggressive behavior were confined to trials between individuals of the same sex (Table I). In no case did a male attack a female or *vice versa*. The probability of this occurring on the basis of chance alone, and not due to the sex of the animals being tested is equivalent to one half to the twelfth, or .00024. Observation of the suspended panel corroborated the findings of the laboratory pairings. In eighteen days of free movement the seventeen subjects showed no tendency to reaggregate as clones, but in four instances individuals paired off in

TABLE I

Interclonal aggressive encounters

	Clone	#1	#2	#3	#4	#5
Female	#5	0	0	2	3	
Female	#4	0	0	2		
Female	#3	0	0			
Male	#2	5				
Male	#1					

direct tentacle to tentacle contact with nonclonemates of the opposite sex for the duration of the eighteen day period. Nonclonemates of the same sex were never found in contact.

DISCUSSION

Metridium senile, unlike *Anthopleura elegantissima*, does not spawn synchronously throughout a colony (Abbot, Hopkins Marine Station, pers. comm., 1982). When gametes are released by individuals in an asynchronous manner into the marine environment, the problem of achieving successful fertilization may be considerable if an animal is surrounded by individuals of its own sex and its gametes are quickly dispersed. A mechanism enabling a clonal coelenterate to discover the sex of its neighbors and cause like sexed nonclonemates to move away so that opposite sexed nonclonemates can approach would greatly increase the probability of successful fertilization. Interclonal/intrasexual aggression in *Metridium senile* may be just such a mechanism. Following three active mixed sex trials, a second examination of the gastrovascular cavity of each of the three females yielded both live sperm and well developed eggs, where previously only eggs had been found. In no other case were the two found within one animal. Internal fertilization has not previously been reported to occur in this species. It is possible that catch tentacles are not only used for intrasexual aggression, but may function in "courtship" as well, enabling two anemones to release their gametes at the most propitious moment. This is the impression given by observation of the long slow catch tentacle interactions occasionally seen in mixed sex pairs of *Metridium senile*, as they touch and probe one another's oral surfaces, and draw closer and closer together.

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